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Development of Nodal and Lateral Roots in Potato under Field Conditions

Kazuto IWAMA
Botany and Agronomy, Faculty of Agriculture,
Hokkaido University, Sapporo 060, Japan
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Abstract

Development and distribution of nodal and lateral roots under field conditions were investigated using two to four varieties of potato. Approximately 90% of nodal roots had already emerged by the fourth leaf stage, thereafter, their diameters increased. Maximum values of both number and diameter of nodal roots were achieved during the initial flowering stage. Within up to 30 cm of soil from the surface, the number of first-order lateral roots per cm of nodal root was about 9, while the number of second-order lateral roots per cm of first-order lateral root was about 4. Diameters for both lateral roots were almost the same, 0.2-0.3 mm, much thinner than the diameters of nodal roots, which were about 1.0 mm. Maximum root extension depth in soil during the growing season was about 60 cm for early varieties and 100 cm for late varieties. The roots, especially the lateral roots, concentrated at the site just beneath hill center at depth of 10-20 cm, where fertilizers had been applied. About 97% of total root length, to a depth of 100 cm, consisted of lateral roots. Average specific root length (length per unit dry weight) was 17 m g^{-1} for nodal roots and 295 m g^{-1} for lateral roots.
Key words: Number of roots, Root diameter, Root distribution, Root morphology, *Solanum tuberosum* L., Varietal differences.

Introduction

The characteristic features of potato root systems differ from those of other field crops. For example, root extension depths under various soil conditions ranged from 50 to 120 cm[1-9]. This was generally shallower than extension depths for roots of other field crops[10-13]. Total root length and dry weight (DW) throughout the soil profile were also smaller for potato plants. In a comparison of 6 crops (maize, wheat, soybean, sugarbeet, rice and potato), Yamaguchi and Tanaka[13] reported that potato had the smallest total root length and DW. Knowledge of the formation of the potato root, however, especially its morphological aspects (e.g. a number and diameter of roots), is very scarce. The purpose of the present report was to investigate development of nodal and lateral roots of the potato under field conditions and their relationships with distribution of root length and DW in soil.

Materials and Methods

The data consisted of the results from 4 experiments conducted at the Hokkaido National Agricultural Experiment Station at Shimamatsu (volcanic-ash sandy-loam soil, 42 °N), Hokkaido. In each experiment 2 to 4 varieties or breeding lines of potato were planted at intervals of 40 cm within rows and 75 cm between rows. A combination of fertilizers at the rate of 1000 kg/ha of 12-18-12 (N, P_2O_5, K_2O) was banded beneath the mother tubers just before planting.

Experiment 1

To investigate the number and diameter of nodal roots (roots emerged from the underground stem nodes), 4 varieties ('Priekulskii-rannii', very early maturity ; 'Danshakuimo' ['Irish Cobbler'], early maturity ; 'Shiretoko'; 'Norin 1', late maturity) were planted on May 23, 1977. Root samples for each variety were taken from 4 hills with 3 replications at 3 stages : the fourth leaf stage (11 days after sprouting, DAS); the initial flowering stage (39 DAS); and the full leaf expanding stage (53-68 DAS). After excavating the roots to a depth of 30 cm in soil and washing them, a maximum diameter at the site of 5 cm from the base of nodal root and a number of nodal roots per stem were recorded.

Experiment 2

To investigate diameters and numbers of lateral roots, 2 late varieties ('Norin 1' and 'HK 61') were planted on May 18, 1980. A soil monolith (width : 5 cm ; length : 30 cm ; depth : 30 cm) was dug in late August from the center of the row for each variety. After washing soil and plant residues, a dissecting scope was used to measure diameters of each root member (nodal root, and first- and second-order lateral root) and numbers of higher-order roots which had branched from nodal or first-order lateral roots in each 10-cm depth soil layer. The total number of root diameter observations was 46 for nodal roots, 230 for first-order lateral roots and 140 for second-order lateral roots.

Experiment 3

To investigate horizontal distributions of root DW within soil up to a depth of 30 cm from the surface, 2 varieties ('Danshakuimo' and 'Norin 1') were planted on May 15, 1978. All soils for 3 adjacent hills in a row of each variety were excavated separately at sites at the center of the hill (Intra-hill, 20×20 cm), between the hills (Inter-hills, 20×20 cm) and between the rows (Inter-rows, 55×40 cm) at 6-7 stages during the growing season (Fig. 1). They were washed with running water and the roots were collected in a sieve with 1-mm mesh openings. Root DW was recorded after oven drying at 80 ℃ for 48 hours.

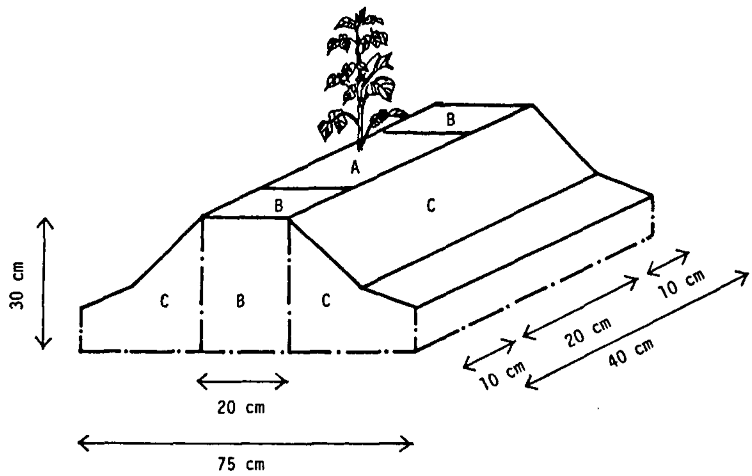

Fig. 1. Diagram of sampled soil blocks within a hill in Exp. 3.
Note. A : Intra-hill, B : Inter-hills, C : Inter-rows.

Experiment 4

To investigate root length distribution throughout the soil profile to the depth of 100 cm, 2 early varieties ('Danshakuimo' and 'Toyoshiro') and 2 late varieties ('Norin 1' and 'HK 61') were planted on May 18, 1980. Twelve soil-root cores (per-core volume : 100 cm^3, length : 5 cm) were collected within each 10-cm depth increment at sites of 0, 15 and 30 cm from the center of hill in each variety in early July (the initial flowering stage), in early August (the full leaf expanding stage for the early varieties) and in late August (the full leaf expanding stage for the late varieties). After washing them with running water and collecting the roots in a sieve with 1-mm mesh openings, Tennant's method[14] was used to measure root length, thereafter, root DW was recorded.

Results

1. Number and diameter of nodal roots

Figure 2 shows changes over time in numbers of nodal roots which had emerged from the upper and lower nodes of underground stems. Although the maximum number of nodal roots per stem node during the growing season was generally 5 to 7, most of the nodes, except for one or two nodes just below the soil surface, had already produced their maximum number of nodal roots by the fourth leaf stage in late June. Since the number of nodal roots on the nodes just below the soil surface increased after ridging in late June, the maximum number of nodal roots per stem (35 to 40) was achieved by the initial flowering stage in middle July. Thereafter, the number decreased because of the deaths of nodal

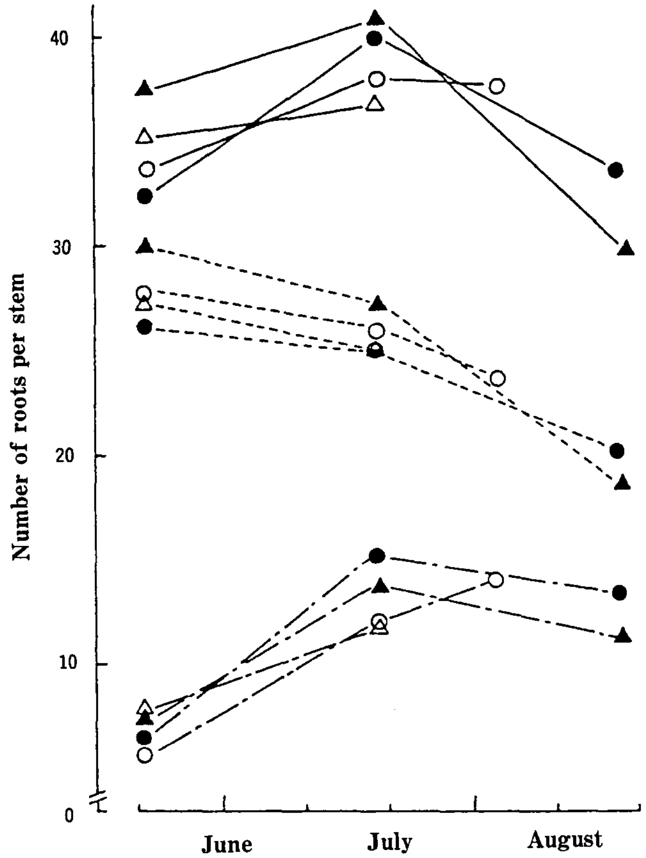

Fig. 2. Changes over time in the number of nodal roots per stem in Exp. 1.
Note. △ : 'Priekulskii-rannii', ○ : 'Danshakuimo', ▲ : 'Shiretoko', ● : 'Norin 1'. ——— : All nodes, --- : Lower nodes, —·— : Upper nodes. The nodes of the underground stem were divided into two parts, upper and lower, taking the third node from the soil surface as the boundary for the upper nodes.

roots on the nodes near the mother tuber. As the mean number of stems per hill for each variety was 3.0 to 4.4, the number of nodal roots per hill in the initial flowering stage was 89 to 145.

Figure 3 shows the changes over time in diameters (maximum value per hill) of nodal roots emerging from upper and lower nodes on the underground stem. Diameters increased until the initial flowering stage, reaching maximum values of 0.6–1.1 mm for upper nodes and 0.9–1.6 mm for lower nodes. It tended to be larger in the late varieties because of a larger increase from the fourth leaf stage to the initial flowering stage.

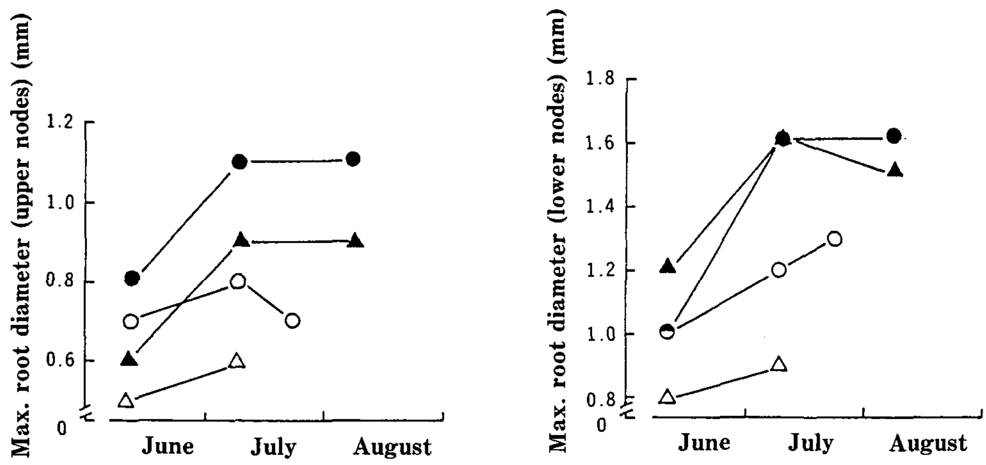

Fig. 3. Changes over time in the maximum diameters of nodal roots per hill for upper nodes (left) and lower nodes (right) of underground stems in Exp. 1.
Note. Varietal symbols are the same as those shown in Fig. 2.

Table 1. Mean values of two late varieties for the diameters of nodal and lateral roots, and the numbers of first- or second-order lateral roots per cm of nodal or first-order lateral roots in Exp. 2.

Soil depth (cm)	Nodal root: Diameter (μm)	Nodal root: Number of 1st laterals (cm^{-1})	1st-order lateral root: Diameter (μm)	1st-order lateral root: Number of 2nd laterals (cm^{-1})	2nd-order lateral root diameter (μm)
0–10	1094 (432)	9.5 (1.7)	245 (95)	4.7 (2.7)	134 (23)
10–20	979 (267)	9.2 (2.2)	264 (54)	4.9 (2.2)	306 (114)
				*5.8 (2.3)	*360 (105)
20–30	1067 (228)	6.9 (2.0)	315 (89)	2.5 (1.4)	214 (37)
Mean	1063 (360)	8.7 (2.2)	270 (86)	4.1 (2.3)	245 (118)

Note. Values in parentheses represent standard deviation.
*Values particularly at the site where fertilizers were applied.

2. Number and diameter of lateral roots

Table 1 shows the diameters of nodal roots, first- and second-order lateral roots , and the numbers of higher-order roots which had branched from nodal or first-order lateral roots in late August. Since the varietal differences for these characters were not significant in two late varieties, the mean values of the varieties within each 10-cm depth increment are shown in the table. The root diameters in three depths were approximately 1.0 mm for nodal roots and 0.2-0.3 mm for first-order lateral roots. The difference in diameters between the first- and second-order lateral roots was not significant.

The numbers of first-order lateral roots per cm of the nodal root in three depths were 7-10, while the numbers of second-order lateral roots per cm of first -order lateral root were 3-5. They tended to be smaller for 20-30 cm than for 0-10 cm or 10-20 cm. Although there were usually few third-order lateral roots branching from second-order lateral roots, there were many third-order lateral roots at the site just beneath the mother tuber at 10-20 cm depth, where fertilizers

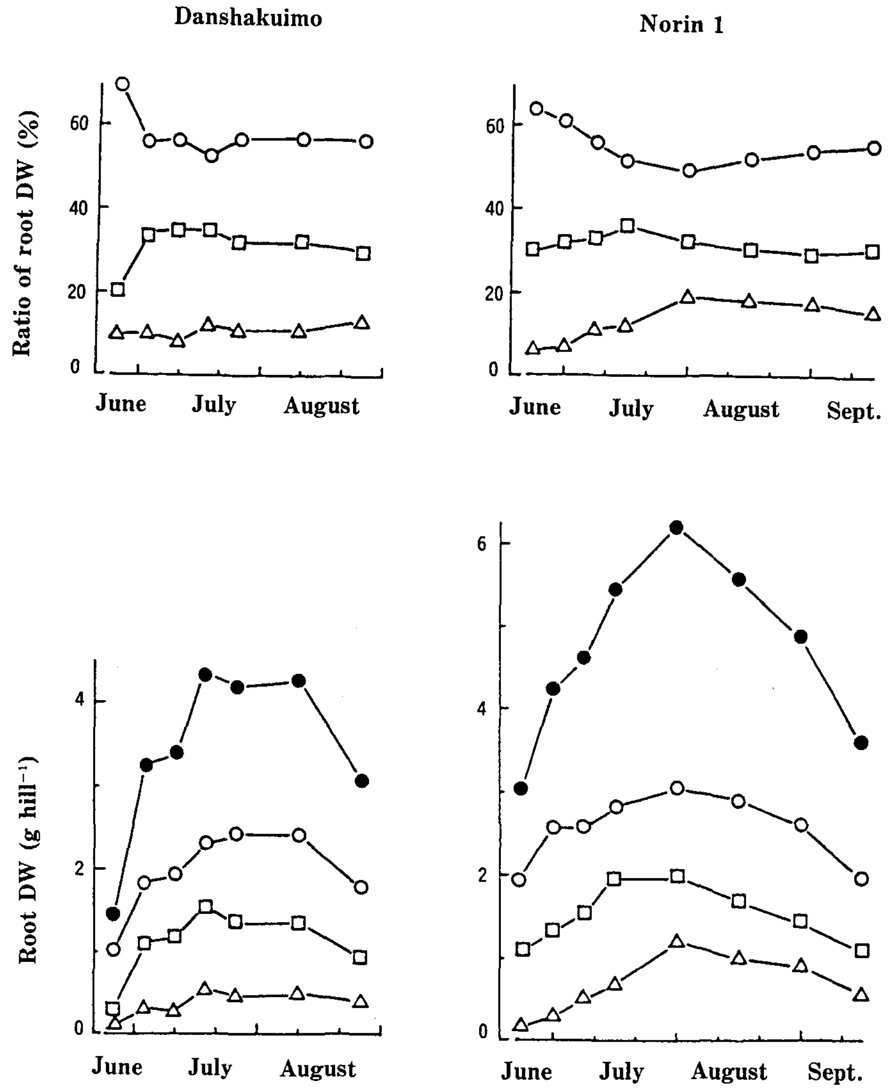

Fig. 4. Changes over time in root DW for different soil blocks in a row to a depth of 30 cm in Exp. 3.
Note. ● : Total root DW, ○ : Root DW at Intra-hill, □ : Root DW at Inter -hills, △ : Root DW at Inter-rows.

had been applied. Fourth- and fifth-order lateral roots were also found at this site. The diameters of these higher-order lateral roots were similar to those of second-order lateral roots.

3. Distribution of root DW and length

Figure 4 shows changes over time in root DW of horizontally different soil blocks from the hill center at depth of 0-30 cm. The increase of root DW from sprouting (early June) to late June was the largest in the soil block taken from the Intra-hill in both varieties. Thereafter, root DW in all blocks, except for the Inter-rows of 'Danshakuimo', increased and reached their maximum values in mid July for 'Danshakuimo' and early August for 'Norin 1'. The increase of root DW at the Inter-rows of 'Danshakuimo' was small. Although total root DW per hill was much larger for 'Norin 1' than 'Danshakuimo' throughout the growing season, the difference in root DW was consistently seen in all soil blocks. The percentage of root DW to total root DW remained relatively constant in each soil block throughout the growing season, with the exception of the early stages of both varieties. It was 50-60% at the Intra-hill, 30-40 % at the Inter-hills and 10-20% at the Inter-rows.

Table 2 shows the root length in each soil layer during the growing season. The roots of 2 late varieties penetrated to a depth of 60 cm in early July and 80

Table 2. Roots length (m $hill^{-1}$) in each soil layer in Exp. 4.

Variety	Soil depth (cm)										
	0−10	10−20	20−30	30−40	40−50	50−60	60−70	70−80	80−90	90−100	Total
Early July											
Danshakuimo	217	699	122	37	4	0	0	0	0	0	1079
Toyoshiro	322	959	254	58	22	0	0	0	0	0	1615
HK 61	348	784	96	58	16	0	0	0	0	0	1301
Norin 1	258	900	110	26	8	9	0	0	0	0	1311
Mean	286	836	145	45	12	2	0	0	0	0	1326
%[1]	21.6	63.0	11.0	3.4	0.9	0.2	0.0	0.0	0.0	0.0	100
Early August											
Danshakuimo	130	955	137	170	18	13	0	0	0	0	1422
Toyoshiro	383	968	162	203	10	11	0	0	0	0	1737
HK 61	307	1194	259	78	8	10	2	1	0	0	1858
Norin 1	245	758	256	160	62	7	7	4	0	0	1499
Mean	266	969	203	153	25	10	2	1	0	0	1629
%[1]	16.3	59.5	12.5	9.4	1.5	0.6	0.1	0.1	0.0	0.0	100
Late August											
HK 61	228	1166	257	69	79	66	6	5	4	1	1882
Norin 1	251	1320	276	145	86	34	9	3	3	3	2128
Mean	240	1243	267	107	83	50	8	4	3	2	2005
%	12.0	62.0	13.3	5.3	4.1	2.5	0.4	0.2	0.2	0.1	100

Note. 1) Percentage of each root length to total root length.

cm in early August. The penetration depths of 2 early varieties were 10-20 cm shallower than those of the late varieties. Thereafter, the late varieties continued the root penetration to deeper depth and reached 100 cm by late August.

The increase of root length for all varieties was greatest during one month after the sprouting. In early varieties, 85% of the maximum root length for the growing season had already developed by early July. In late varieties, 66% of the maximum root length had developed by that date. In addition, approximately 60% of the total root length in soil to a depth of 100 cm was concentrated at depth of 10-20 cm in all varieties on all sampling dates. The root lengths in depths of 30-100 cm were less than 15% of the total root lengths in all varieties.

Figure 5 shows a summary of distribution patterns for the root system in early August throughout the soil profile. The root length density (root length

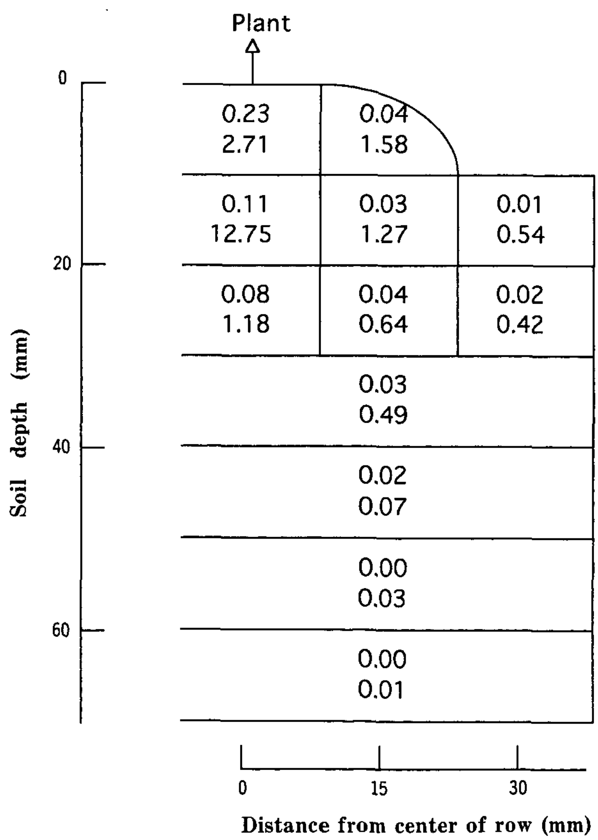

Fig. 5. Root length density (cm cm^{-3}) throughout the soil profile in early August in Exp. 4.
Note. The upper and the lower numerals in each soil layer are for nodal roots and the lateral roots, respectively. All values are the mean of 4 varieties.

per unit soil volume, RLD) for nodal roots was the highest in the depth of 0-10 cm beneath the hill center, and gradually decreased vertically and horizontally distant from the center of hill. The RLD for lateral roots was much higher than that for nodal roots throughout the soil profile. The percentage of the lateral root length to the total (nodal+lateral) root length was 97.3% within the depth of 0-30 cm and 96.7% throughout the soil profile. In the depth of 10-20 cm beneath the hill center, in particular, where fertilizers had been applied, lateral roots showed extremely dense development and maximum RLD value (13 cm cm^{-3}) for the entire soil profile was found. Lateral roots decreased significantly below 30 cm.

Table 3 shows the relationships between root length and root DW among the data for 4 varieties throughout the soil profile in early July and in early August.

Table 3. Simple correlation coefficients between root DW and root length throughout the soil profile for all varieties in Exp. 4.

Samping date	Correlation coefficient	Regression line y : Root length (m), x : Root DW (g)
Early July		
All roots	0.937***	y=200.3 (±20.9)x
Early August		
All roots	0.972***	y=236.6 (±16.3)x
Nodal root	0.947***	y= 16.5 (±2.2)x
Lateral root	0.986***	y=294.8 (±19.0)x
Total	0.952***	y=217.3 (±13.7)x

Note. Values in parentheses represent the 95% confidence limit of the regression coefficient.
***: Significance at 0.1% level.

A strong correlation was found between two traits. Coefficients of the regression lines in early August indicated that the specific root length (root length per unit root DW) was 17 m g^{-1} in the nodal roots and 295 m g^{-1} in the lateral roots.

Discussion

Potato roots consist mainly of nodal and lateral roots. Although some roots emerged from the nodes of stolons, especially in varieties of late maturity and some wild relatives[15], they were far fewer than those for nodal and lateral roots. In addition, although Kratzke and Palta[16] reported that roots emerged from tuber surfaces, such roots were not found in the present experiments.

Literature describing the root morphology of potato plants is limited. Kawatei et al.[4] reported that the underground stem of 'Danshakuimo' had 6 to 8 nodes and approximately 5 nodal roots per stem node, totalling 28 to 45 nodal roots per stem. Weaver[12] reported that the number of nodal roots per stem was

55. In the present study, it was found to be 35 to 40. In addition, in an experiment in which 10 varieties were observed[17], it was 23 to 40. Although the reported numbers of nodal roots seemed to vary, the range of variation was thought to be relatively small when the large differences in environmental conditions and varieties in which these experiments were conducted were considered.

It is of interest to note that the change over time in the number of nodal roots differed between potato plants and cereals. It is well known that the emergence of nodal roots in cereals is usually synchronous with the emergence of leaves[18]. The present results, however, showed that approximately 90% of the nodal roots had already emerged by the fourth leaf stage, indicating that most of nodal roots start to grow much earlier than leaves. Similar results have also been reported in previous studies[4,12]. It is therefore considered that there is no synchronous relationship between the emergences of nodal roots and leaves in potato plants.

It is also interesting to note that the increase of total root DW per hill during the growing season tended to show no relation to the number of nodal roots. Although root DW increased significantly from the fourth leaf stage to the initial flowering stage, the increase of the number of nodal roots was small. On the other hand, the nodal root diameter showed a relatively large increase during this period. The difference in total root DW per hill among 10 varieties[17] also showed a strong correlation with the nodal root diameter, but not with the number of nodal roots. These results indicate that differences in total root DW of potato plants between growth stages and also between varieties are closely related to those in nodal root diameter.

The distributions of root length and DW throughout the soil profile in the present results differ somewhat from the famous description given by Weaver[12]. He argued that potato roots penetrate horizontally during early growth and then turn downward. In his data, root growth was very sparse in the soil beneath the hill center. In the present study, however, the roots, especially the lateral roots, concentrated at the site beneath the hill center at depth of 10-20 cm. Lesczynski and Tanner[5] also reported similar results. It can be supposed that these differences in root distribution patterns may be due to the growth of lateral roots. In the present study, fertilizers were banded just beneath the mother tuber, where fifth-order lateral roots were observed. Sattelmacher et al.[19] reported that increases in nitrogen levels in the solution culture of potatoes greatly stimulated the growth of lateral roots. His results partly support the present findings.

The present study has also shown that there is a large varietal difference in the depths of root extension. It was 10 to 20 cm deeper for the late varieties than the early varieties in early July and early August. Although the early varieties were not measured in late August, their maximum root extension depths during the growing season will be 60 cm, as the leaves of early varieties started senescence in middle August. On the other hand, the roots of late varieties continued to extend after early August and reached to depths of 100 cm by late August.

The results indicate that late varieties show higher rate and longer duration of root extension than early varieties. It has already been reported that late varieties have larger root DW than early varieties in potato plants[15,17,20]. It was due to higher rate and longer duration of root DW increases in late varieties than in early varieties[17]. In the present study, these varietal differences in root DW increase were shown at all soil blocks in depth of 0-30 cm (Fig. 4). The results in root DW and extension depth indicate, therefore, that there are differences in both the rates and durations of root growth for entire soil profiles between varieties of different maturity in potato plants.

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(* In Japanese with English summary, * * In Japanese without English summary)